

Comparisons in demographic rates of bay scallops in eelgrass and the introduced alga, *Codium fragile*, in New York

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Abstract Bay scallops, *Argopecten irradians*, supported vibrant fisheries which subsequently collapsed, as such, they are a focus species for many restoration efforts along the Atlantic and Gulf coasts of the United States. The scallops' preferred habitat, seagrass, has also dramatically declined, and some scallop populations have increased post-restoration despite reduced seagrass cover. This has led to the hypothesis that macroalgae may serve as suitable alternative habitats for bay scallops. This study is the first to compare demographic rates, such as long-term survival, growth, condition and reproductive potential of scallops between the native eelgrass, *Zostera marina*, and the introduced alga, *Codium fragile*. Although long-term survival was not different between habitats, results suggest site-specific and inter-annual variation in the impacts of *Codium* on scallop growth. While demographic rates did not differ in Shinnecock Bay, in Sag Harbor, growth and/or condition were significantly different between both vegetated habitats depending on the year. However, recruit density, size and condition did not vary significantly, adding to the complexity of this relationship. Despite potential site-specific and inter-annual differences, this

study supports the hypothesis that habitats other than eelgrass can benefit bay scallops.

Introduction

The bay scallop, *Argopecten irradians* (Lamarck 1819), historically supported vibrant fisheries in many US Atlantic and Gulf coast states before populations collapsed during the past 30 years. Some reasons for the scallop declines include harmful algal blooms (Summerson and Peterson 1990; Tettelbach and Wenczel 1993), habitat loss from eutrophication (Serveiss et al. 2004) and trophic cascades (Myers et al. 2007). In the period since, there has been tremendous interest and effort to restore dwindling scallop populations throughout their geographic range, from Massachusetts to Florida, with varying degrees of success (Peterson et al. 1996; Goldberg et al. 2000; Arnold et al. 2005; Tettelbach and Smith 2009). Some of the variation in restoration success may be linked to the bay scallops' strong habitat association with seagrass (Belding 1910; Gutsell 1930; Thayer and Stuart 1974) which has also declined throughout much of the bay scallops' range (Orth et al. 2006).

Seagrasses have long been considered vital bay scallop habitat (Belding 1910) because they offer a favored substrate for larval attachment (Eckman 1987) and present an above-bottom refuge from predation for juvenile scallops (Pohle et al. 1991; Ambrose and Irlandi 1992; Garcia-Esquivel and Bricelj 1993). Survival is also enhanced within seagrass habitats when compared to unvegetated habitats (Prescott 1990), although this association typically comes at a cost to growth (Irlandi et al. 1995; Bologna and Heck 1999). When seagrasses have declined or disappeared, however, scallop populations have sometimes

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increased (Marshall 1947), or at least maintained low populations (Carroll et al. 2010). Scallop restoration efforts in New York have also been highly successful despite relatively low seagrass abundance (Tettelbach and Smith 2009; Tettelbach et al. 2013), suggesting that habitats other than seagrass may be useful for bay scallops.

Macroalgae, including non-native species, may be alternative habitats for scallops. In the Niantic River, Connecticut, an unidentified branching alga would contain such dense sets of scallops that fishermen referred to it as ‘scallop weed’ (Marshall 1960). In Virginia, it is suggested that the alga *Gracilaria* might be a suitable alternative habitat (Hernandez Cordero et al. 2012), while in New York, previous work has suggested that the introduced *Codium fragile* (Suringar) Harriot, 1889, might offer a similar predation refuge to seagrass (Carroll et al. 2010). *C. fragile* was introduced to the northwest Atlantic from Japan in the mid-1950s (Carlton and Scanlon 1985), and now grows in estuaries from Virginia (Thomsen and McGlathery 2007) to Canada (Begin and Scheibling 2003). It is of particular interest because its upright, canopy-forming structure may offer similar functions to fauna as seagrasses. Considerable literature suggests *C. fragile* has had a positive effect on a number of native fauna (Bulleri et al. 2006; Schmidt and Scheibling 2006; Schmidt and Scheibling 2007; Sauchyn and Scheibling 2009; Jones and Thornber 2010; Drouin et al. 2011). In New York, surveys of scallop recruits have consistently found juvenile and adult bay scallops at 12 sites where *C. fragile* is the dominant vegetation (S. Tettelbach, *pers. comm.*, Department of Biology, Long Island University, Brookville, NY); similar observations have been made in other regional estuaries (M. Chintala, *pers. comm.*, USEPA, Atlantic Ecology Division, Narragansett, RI). Therefore, it is possible that the invasive alga, *Codium fragile*, may be a suitable alternative habitat for bay scallops, as has previously been suggested (Carroll et al. 2010).

The notion that a non-native species might have a positive influence on native fauna has been received attention recently (Rodriguez 2006); however, the only work involving non-native algae and bay scallops has been looking at short-term survival with no consideration for changes in demographics such as growth, condition or reproduction (Carroll et al. 2010; Hernandez Cordero et al. 2012). Long-term survival or fitness of fauna associated with *Codium fragile* assemblages has not been previously investigated. Scallops have been demonstrated to exhibit reduced growth in structurally complex seagrass meadows (Irlandi et al. 1995; Bologna and Heck 1999; Irlandi et al. 1999). Mussels also show reduced growth in seagrass patches compared to outside seagrass (Reusch 1998). Given that bivalves, including scallops, experience a cost for growth and condition for associating with vegetated habitats, it is possible that the dense, branching canopy

formed by *Codium fragile* may also influence scallop growth, condition and/or reproductive output.

There has been a recent general hypothesis in regard to bay scallop restoration efforts which suggests that substrates other than eelgrass may be viable alternative habitats (Carroll et al. 2010; Hernandez Cordero et al. 2012). However, *C. fragile* forms a thick algal canopy which has more complexity than eelgrass (Drouin et al. 2011), and since food quantity and/or quality can be reduced in these highly complex habitats, this could have implications on bay scallop life history traits linked to food quantity/quality such as growth and reproductive output (Kirby-Smith 1972; Cahalan et al. 1989; Rheault and Rice 1996). Additionally, strong and significant negative consequences have been shown in invasive algae–bivalve interactions (Wright et al. 2007; Gribben et al. 2009), highlighting the possibility that there could be long-term consequences for scallops associating with *C. fragile* which have as yet gone uninvestigated. A problem with the previous studies, however, is that they failed to examine the negative impacts of an invasive alga on the fitness of native fauna in comparison with native habitats, such as seagrasses. Since bivalves experience a cost of growth in native habitats with which they associate, it is possible that the negative impacts of an invasive alga on growth and condition of bivalves may be exaggerated.

Bay scallops are a focal species for numerous restoration efforts and have high commercial value, so understanding what effects *Codium fragile* might have on scallop populations, especially in comparison with native habitats, has become increasingly important. The objective of this study was to examine the impacts of the invasive macroalga, *Codium fragile*, on demographics (growth, condition) of the northern bay scallop, *Argopecten irradians irradians*. Specifically, we expected that growth and condition would be lower in both vegetated habitats than unvegetated, bare sand, but would not be different from each other, and that this pattern would be similar between sites with different hydrodynamics. As a secondary hypothesis, we predicted that any differences would be due to food quantity differences among the habitats. During year two, we predicted that differences would be due to epibiotic load levels among the habitats. We compared long-term (>10 weeks) survival, growth and condition of juvenile scallops in *C. fragile*, eelgrass and unvegetated habitats at two sites during 2 years.

Methods

Study sites

This study was conducted at two sites which both had three distinct habitats—Eelgrass (*Zostera marina* L 1753), Sand

and *Codium fragile*—in the estuaries on the east end of Long Island, NY. The first study site, Shinnecock Bay, is a small, shallow, lagoon estuary located on the South Shore of Long Island, separated from the Atlantic Ocean by a barrier beach and receiving ocean water through a maintained inlet. It is characterized by sandy sediments and, currently, has some of the most extensive eelgrass meadows in New York. Experimental sites for habitat-specific growth were located along the northeastern shore of the bay. ‘Eelgrass’ (41°01.030’N, 072°16.986 W), ‘Sand’ (01.030’N, 16.978 W) and ‘*Codium*’ (01.027’N, 16.994’W) habitats were within 1,000 m along the same exposed shoreline, and at similar depths (~1–1.5 m MLW). The eelgrass site was sandy, with 373 ± 81 shoots per m², and areal cover ranging from 67 to 85 %. The sand site contained little algal percent cover (less than 5 %) which mainly consisted of drifting bits of red macroalgae of either *Gracilaria* sp. or *Aghardiella* sp., and *Spyridea* sp., as well as bits of *Ulva lactuca* that landed within the quadrat. The *C. fragile* site was also sandy, with *C. fragile* thalli attached to clumps of *Crepidula fornicata*, dead clam shells, and larger cobble and rocks, and had between 58 and 100 % percent cover. The second site, Sag Harbor (41°01.108’N, 072°16.913’W; Fig. 1), was chosen for three reasons: (1) it was the site of previous short-term survival experiments, (2) the Peconic Estuary offers different hydrological features, resembling a drowned river valley with deep tidal channels and shallow banks, and (3) scallop populations have been increasing at this location. The Sag Harbor study site was deeper (2–3 m MLW), but contained all three habitats being investigated (see Carroll et al. 2010 for a full site description). While there were numerous

locations around Long Island which either eelgrass or *C. fragile* serve as the dominant vegetation, sites were selected where both vegetated habitats exist within close proximity.

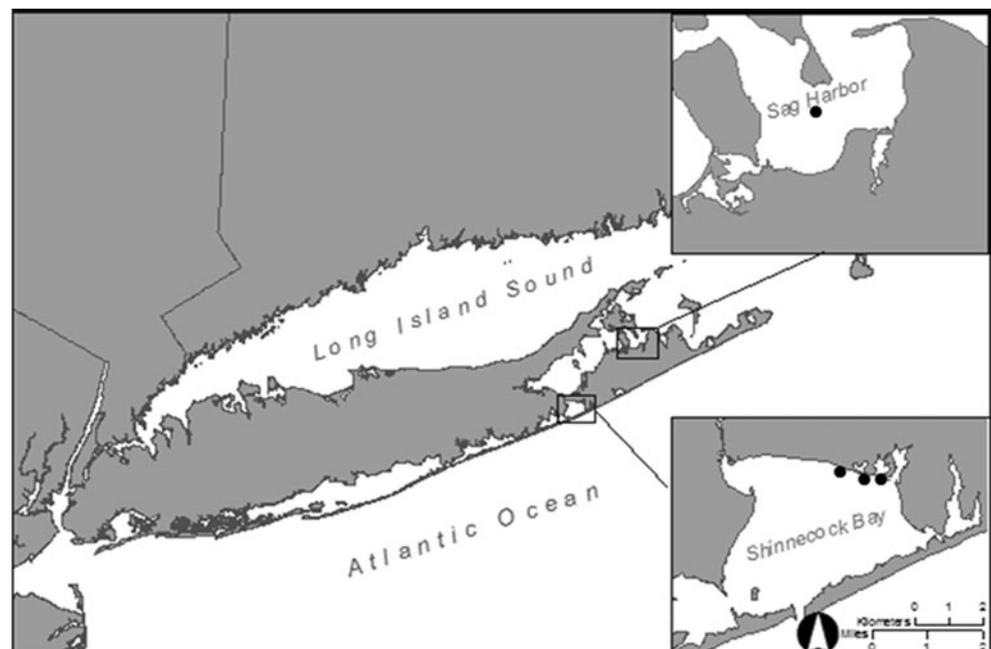
Juvenile growth and condition

Groups of wild set scallops, collected via spat bags during monitoring for the large-scale restoration efforts in the Peconics (see Tettelbach et al. 2013), were placed within cages (35 × 17 × 8 cm) constructed from 8-gauge, coated wire and enclosed in a 1-mm mesh bag. Cages were anchored directly to the bottom in all habitats using rebar stakes, so that scallops were separated from seafloor by the 1-mm mesh bag. Sets of 10 scallops were marked by gluing numbered white wire tags to the dorsal valve, then measured to the nearest 0.1 mm before deployment and placed into the cages. Five replicate cages were uniquely labeled and placed into each habitat, for a total of 50 labeled, caged scallops within each habitat. This was repeated for both sites and both years, for a total of 50 scallops per habitat per site per year ($n = 600$ scallops across both sites over both years). Cages were deployed 10 weeks in 2009 and 11 weeks in 2010. At the end of the deployment period, cages were retrieved, and all living scallops were identified (if possible) and measured to the nearest 0.1 mm. Growth rates were calculated using the following equation:

$$\text{Growth rate} = \frac{(\text{final shell height} - \text{initial shell height})}{\text{days}} \quad (\text{Shriver et al. 2002}) \quad (1)$$

Since shell and tissue growth may be uncoupled for bivalves (Lewis and Cerrato 1997), scallop tissues were

Fig. 1 Map of the study sites on Long Island, New York, the United States. Insets show the study areas, indicating the locations of Sag Harbor, NY, and Shinnecock Bay, NY. Circles indicate the study sites



then removed into pre-weighed aluminum boats and dried to constant mass at 70 °C for at least 48 h. Condition indices were computed using the following equation:

$$CI = \left(\frac{\text{tissue dry weight}}{\text{shell height}} \right) \times 100 \quad (\text{Rheault and Rice 1996}) \quad (2)$$

Low values indicate that energy reserves have been depleted for maintenance under poor environmental conditions (Martinez and Mettifugo 1998). Shell strength is related to shell weight (Zuschin and Stanton 2001) and can vary with environmental conditions (Nagajaran et al. 2006), so shell weights normalized by shell height were used as an additional fitness parameter and a proxy for shell strength.

Epibiont load

In 2009, qualitative differences in fouling organisms on the scallop shells led to epibiont load quantification in 2010. At the end of each experiment, the epibiont community from both valves of every scallop within each cage was scraped into pre-weighed aluminum tins. Since the number of scallops at the end of the experiment varied with survival, the epibiont load biomass was standardized per scallop.

Chlorophyll analysis

Since food supply was the hypothesized factor contributing to differential growth in the various habitats, in 2009, water samples were collected from within vegetated canopies using 60-mL syringes and from near-bottom (~10 cm) in unvegetated habitats using sample bottles by SCUBA divers, with 6 collections per habitat. Temporal spacing of water samples was approximately every 2 weeks during the period of scallop deployment, a sampling period used in previous field growth studies (Shriver et al. 2002). Syringes were filtered onto replicated GF/F filters and 5- μm polycarbonate filters, frozen, extracted in acetone and measured for fluorescence with a Turner fluorometer (Parsons et al. 1984). Differential filtration allowed the amount of chlorophyll in the >5 and <5 μm size fractions to be determined. Both total and size fractionated (<5 μm) chlorophyll *a* were measured since scallops filter different sizes of phytoplankton with varied efficiency.

Reproductive output

In the first year of the study, sets of adult scallops were placed into the three habitats in Shinnecock Bay to investigate the impacts of habitat on gonad development (Sastry 1968). This was only conducted in Shinnecock Bay due to the availability of scallops, obtained from hatchery stock

and overwintered on long lines in Orient Harbor as part of a bay scallop restoration effort in New York (Tettelbach and Smith 2009). Sets of 6 year-old scallops were placed into the cages described above and covered with 10-mm mesh to prevent access by large predators. Initially, a subset of 30 randomly selected scallops were killed for initial shell heights, condition and gonad indices on June 11, 2009. At subsequent 2-week intervals starting June 25, 2009, for a period of 10 weeks, two cages containing scallops were removed from each habitat. Scallops were measured for shell height and dissected. Gonads were removed and placed into a set of pre-weighed aluminum boats; the remaining tissues were placed into another set of corresponding tins. Condition indices were computed as described above. The gonad condition index (GI) was computed using the following equation:

$$GI = \left(\frac{\text{gonad dry weight}}{\text{total tissue dry weight}} \right) \times 100 \quad (\text{Barber and Blake 1991}) \quad (3)$$

Scallops were placed into the various habitats in June 2009 and tracked for 10 weeks through the end of August, encompassing a period of time when gonad development was expected to peak, and spawning was expected to have occurred (Taylor and Capuzzo 1983; Tettelbach and Weinstock 2008).

Natural recruitment scallops

In addition to experimental scallops, a total of 12 haphazardly placed 0.25-m² quadrats were used at the conclusion of the growth studies to determine densities of naturally recruited set and adult scallops in the various habitats in year 2. All seed scallops in the quadrats were collected for processing (Sag Harbor site only). This site was selected because the Peconic Estuary was the site of intense restoration efforts and increased natural populations of scallops (Tettelbach and Smith 2009). Additional scallops were haphazardly selected until a total of 20 seed scallops from each habitat were collected. Shell heights and condition indices were obtained using the methods previously described. Collection occurred in November 2011, at the conclusion of the growth study, during a period of time when fall surveys of juvenile scallops, which settled during the summer, are monitored for the restoration effort (Tettelbach and Smith 2009).

Statistics

Due to significant interactions while conducting a three-way ANOVA for each variable, variables were analyzed separately by site using a two-way ANOVA (cages as the replicates) with year (random) and habitat (fixed) as the explanatory factors and survival, growth rate, condition, or

shell weight/shell height as the response variables. For epibiont load, only recorded in 2010, one-way ANOVAs were run for each site with habitat as the factor. For reproductive output and chlorophyll *a* data, a series of one-way ANOVAs were run due to a significant date x habitat interaction during analysis using two-way ANOVAs. For natural set scallops, density, size, condition and shell weight/shell height were the response variables in a series of one-way ANOVA comparing habitats. When necessary, data transformations were performed to meet the assumptions of normality and equal variance. For survival, which was a proportion, data were arcsine square root transformed. For growth, condition and epibiont load, data were natural log square root transformed. Differences between groups were assessed using the Holm–Sidak multiple comparisons test.

Results

Juvenile scallop growth and condition

Shinnecock Bay—survival across all three habitats was significantly higher in 2009 (92.4 ± 2.4 %; mean \pm SE) than in 2010 (72.2 ± 2.6 %, two-way ANOVA, $F_{(1,22)} = 32.653$, $p < 0.001$). Scallop survival was also affected by habitat ($F_{(2,22)} = 10.329$, $p < 0.001$) across both years; survival in both *Codium fragile* (91.0 ± 2.9 %) and eelgrass (84.6 ± 3.0 %) was higher than survival on sand (71.3 ± 3.3 %, $p < 0.001$ and $p = 0.006$, respectively), but not different from each other ($p = 0.139$). Growth rate did not vary by year (two-way ANOVA, $F_{(1,22)} = 1.501$, $p = 0.234$), but did vary by habitat ($F_{(2,22)} = 9.146$, $p = 0.001$). Similar to survival, growth in both eelgrass (0.335 ± 0.005 mm day⁻¹) and *C. fragile* (0.331 ± 0.005 mm day⁻¹) was significantly faster than on sand (0.306 ± 0.005 mm day⁻¹; $p < 0.001$ and $p = 0.002$, respectively), but were not different than each other ($p = 0.561$, Fig. 2).

Condition index did not significantly differ between years (two-way ANOVA, $F_{(1,22)} = 2.519$, $p = 0.127$) but did significantly vary among habitats ($F_{(2,22)} = 19.084$, $p < 0.001$), although that difference depended on the year (year x habitat interaction, $F_{(2,22)} = 5.226$, $p = 0.014$). In 2009, differences in condition among habitats were not significant, while in 2010, scallops on both eelgrass (2.25 ± 0.09) and *C. fragile* (2.09 ± 0.08) were in significantly better condition than those on sand (1.45 ± 0.09 ; $p < 0.001$ for both), but were not different from one another ($p = 0.199$; see Fig. 2). The shell weight to shell height ratio differed by both year (two-way ANOVA,

$F_{(1,22)} = 14.185$, $p = 0.001$) and habitat ($F_{(2,22)} = 5.596$, $p = 0.011$). Scallops had significantly heavier shells in 2010 than in 2009 ($p = 0.001$), and those in eelgrass were heavier than those in sand ($p = 0.003$). *C. fragile* shells were not different than either habitat.

Sag Harbor—survival across all three habitats was significantly higher in 2009 (92.2 ± 3.0 %) than in 2010 (69.8 ± 3.1 %, two-way ANOVA, $F_{(1,21)} = 26.945$, $p < 0.001$), but not different among habitats ($F_{(2,21)} = 2.065$, $p = 0.152$), although there was a significant year x habitat interaction ($F_{(2,21)} = 6.014$, $p = 0.009$). While there was no difference in survival among habitats in 2009 ($p = 0.604$), in 2010, survival was higher in both eelgrass (82.0 ± 4.9 %) and sand (74.0 ± 4.9 %) than in *C. fragile* (53.3 ± 6.4 %, $p = 0.002$ and $p = 0.018$, respectively), but was not different between eelgrass and sand ($p = 0.263$). Growth rate did not vary by year (two-way ANOVA, $F_{(1,21)} = 0.159$, $p = 0.694$), but did vary by habitat ($F_{(2,21)} = 3.778$, $p = 0.040$). Across both years, growth rates were faster in eelgrass (0.364 ± 0.010 mm day⁻¹) than *C. fragile* (0.324 ± 0.011 mm day⁻¹; $p = 0.013$). Growth in sand (0.353 ± 0.011 mm day⁻¹) was not different than either *C. fragile* ($p = 0.075$) or eelgrass ($p = 0.417$, Fig. 2).

Condition index differed between years (two-way ANOVA, $F_{(1,21)} = 9.450$, $p = 0.006$) and among habitats ($F_{(2,21)} = 8.998$, $p = 0.002$). Condition was higher in 2010 (1.93 ± 0.09) than in 2009 (1.56 ± 0.08). Condition of scallops in both eelgrass (1.94 ± 0.10) and sand (1.92 ± 0.10) was significantly better than those in *C. fragile* (1.37 ± 0.11 ; $p < 0.001$ and $p = 0.002$, respectively), but was not different from one another ($p = 0.862$; see Fig. 2). Shell weight was significantly different between years ($F_{(1,21)} = 12.911$, $p = 0.002$) and among habitats ($F_{(2,21)} = 5.263$, $p = 0.014$). Shells were significantly heavier in 2010 ($p = 0.002$) and were heavier in sand than in *C. fragile* ($p = 0.004$), and marginally heavier in eelgrass than in *C. fragile* (0.041).

Epibiont load

The epibiont load was generally higher in Shinnecock Bay and included barnacles, tube building polychaetes (likely *Hydroides* sp.), *Crepidula fornicata*, the colonial ascidian *Botryllus schlosseri*, as well as the solitary ascidian *Molgula manhattensis*. Epibiont load varied between habitats ($F_{(2,12)} = 8.387$, $p = 0.006$); fouling organism biomass was significantly higher on scallops in cages on sand (222 ± 56.3 mg scallop⁻¹) than on either scallops in eelgrass (32.1 ± 16.5 mg scallop⁻¹, $p = 0.001$) or *Codium fragile* (98.0 ± 21.2 mg scallop⁻¹, $p = 0.015$), which

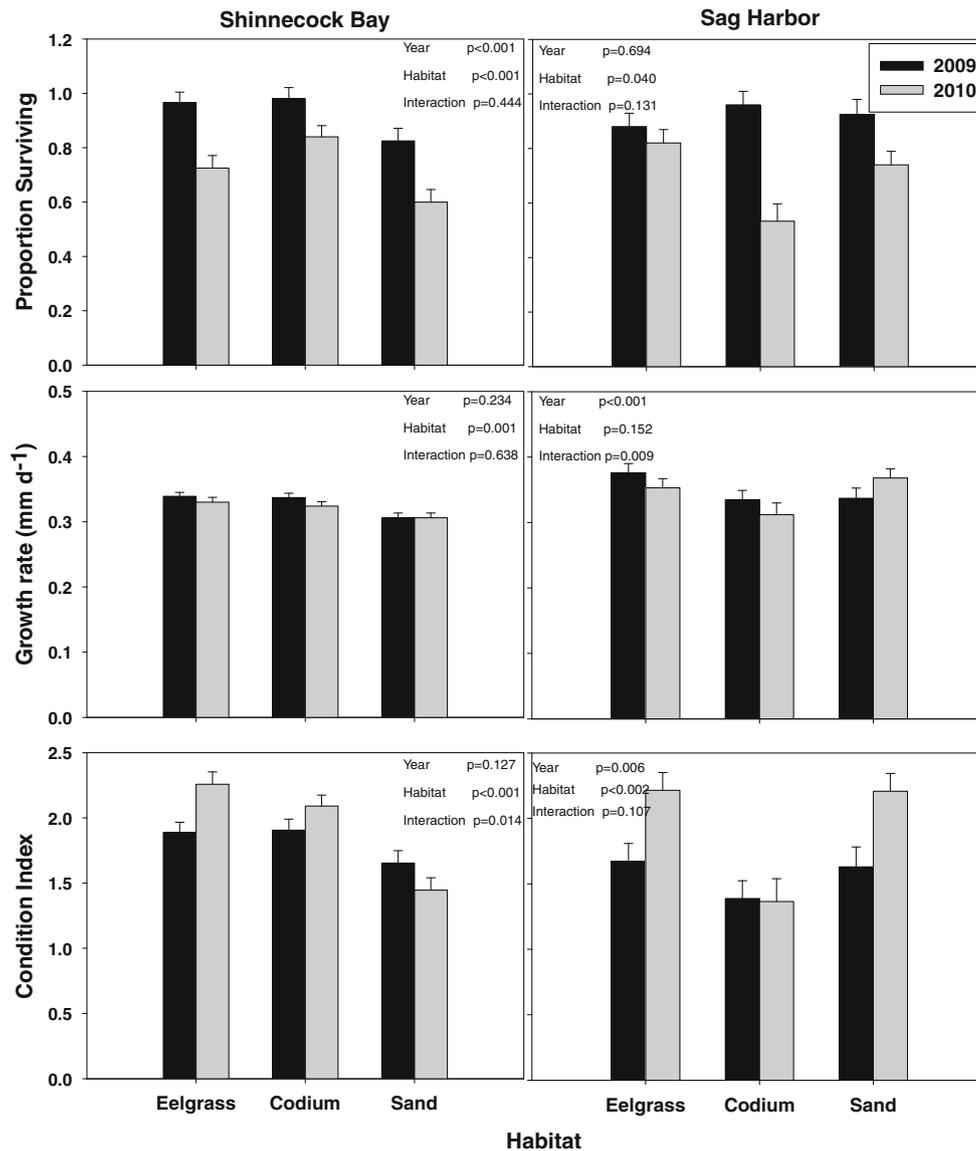


Fig. 2 Survival (proportion surviving), growth (mm day^{-1}) and condition index ($\text{CI} = (\text{tissue dry weight}/\text{shell height}) \times 100$) of juvenile scallops placed in three habitats in Shinnecock Bay and Sag

Harbor, New York, for 10 weeks in 2009 and 11 weeks in 2010, illustrating the results of two-way ANOVA

were not different from each other ($p = 0.102$). There was a significant negative correlation between growth rate and epibiont load in Shinnecock Bay ($\text{Shell Growth} = 25.5 - (9.4 * \text{mass of epibionts per scallop})$, $r^2 = 0.423$, $F_{(1,12)} = 9.815$, $p = 0.010$, Fig. 3a). In Sag Harbor, scallops were generally much cleaner, with the fouling community mostly comprising of small *C. fornicata* and tube worms, with very little fouling by either tunicate species. Epibiont load was not significantly different between habitats ($F_{(1,10)} = 2.851$, $p = 0.116$), and there was a significant positive relationship between growth rate and epibiont load ($\text{Shell Growth} = 23.9 + (370.6 * \text{mass of epibionts per scallop})$, $r^2 = 0.631$, $F_{(1,10)} = 18.072$, $p = 0.002$, Fig. 3b).

Chlorophyll

Both total and $>5\text{-}\mu\text{m}$ size fractionated Chl *a* were highly variable over time and between habitat treatments at both sites, with no habitat having consistently greater Chl *a* concentrations (Online Supplement 1).

Reproductive output

Scallops significantly increased their shell height over the course of the experiment ($p < 0.001$) but this did not differ by habitat ($p = 0.106$). GI was not significantly different among habitats on June 25, 2009 ($p = 0.751$). On 9 July,

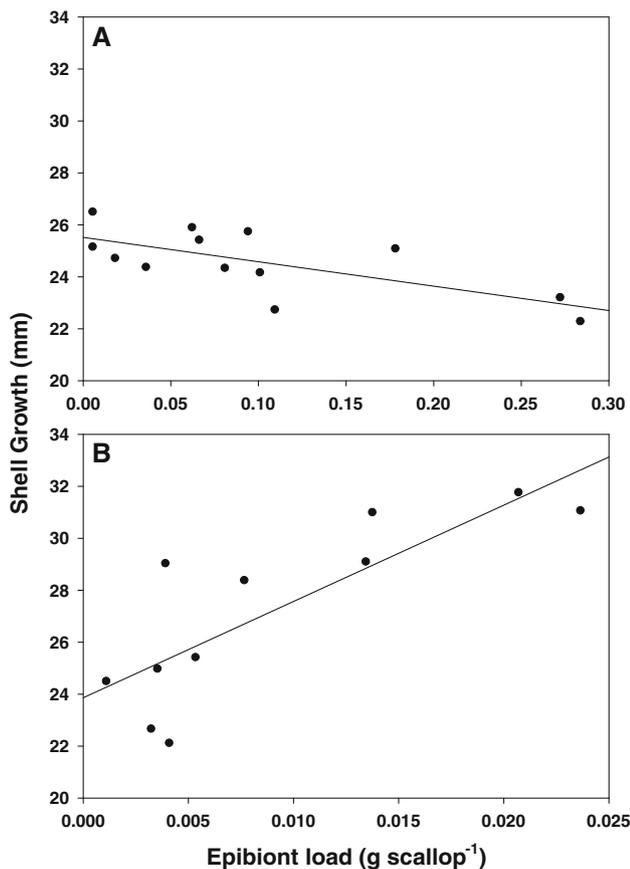


Fig. 3 Linear regressions showing the shell growth (mm) as a function as epibiont load (g of epibiont per scallop) for Shinnecock Bay (A) Shell Growth = $25.5 - (9.4 * \text{mass of epibionts per scallop})$, $r^2 = 0.423$, $F_{1,12} = 9.815$, $p = 0.010$; and Sag Harbor (B) Shell Growth = $23.9 + (370.6 * \text{mass of epibionts per scallop})$, $r^2 = 0.631$, $F_{1,10} = 18.072$, $p = 0.002$. Note that the scale for the mass of epibiont load is not the same

GI was significantly higher in *Codium fragile* (32.0 ± 1.2) and sand (27.8 ± 2.3) than in eelgrass (20.4 ± 1.5 , $p < 0.001$ and $p = 0.006$, respectively). Scallops in sand had significantly higher GI (29.3 ± 1.8) than in both *C. fragile* (20.9 ± 2.1 , $p = 0.003$) and eelgrass (20.3 ± 0.9 , $p = 0.002$) on 23 July. There were no differences among habitats during collections on either 7 August ($p = 0.909$) or 20 August ($p = 0.486$; Fig. 4).

Natural recruit scallops

In Shinnecock Bay, only one scallop was found and occurred in the *Codium fragile* habitat. In Sag Harbor, scallop abundances were higher in both eelgrass and *C. fragile* than in sand; although due to high variability within samples, these differences were not significant ($p = 0.178$). Scallop shell height was not different across the three habitats in Sag Harbor ($p = 0.380$; Fig. 5), nor was CI ($p = 0.669$ for shell height). Shell weights were also the

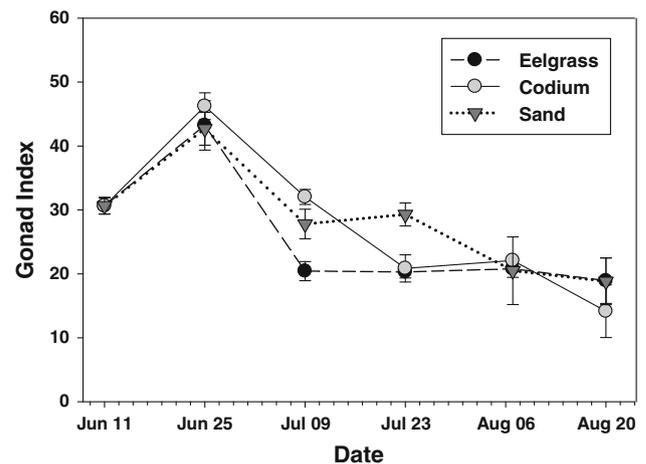


Fig. 4 Gonad indices for scallops placed in the 3 different habitat types in Shinnecock Bay in 2009. Gonad Index (GI) = (gonad dry weight/total tissue dry weight) \times 100, and is a proxy for reproductive output (Barber and Blake 1991). Dashed line with black circles represents scallops in eelgrass, gray circles with solid line is for scallops placed in *Codium fragile*, and gray triangles with dotted lines is for scallops on barren substrates

same between the three habitats ($p = 0.433$). Adult scallops were also collected during the survey, although only 2 were recovered from eelgrass, while 13 were recovered from *C. fragile*, and 0 from sand at the Sag Harbor site. The mean adductor muscle mass in eelgrass was 8.91 ± 0.05 grams, while the mean mass for adults found in *C. fragile* was 8.11 ± 0.63 grams. Unfortunately, the low number found in eelgrass precluded statistical analysis of adult adductor muscle mass.

Discussion

It has been hypothesized that habitats other than seagrass might be useful alternatives for bay scallops which can have important implications on conservation and restoration (Carroll et al. 2010; Hernandez Cordero et al. 2012). However, both previous studies were conducted over shorter time periods and did not investigate demographic rates. Carroll et al. (2010) looked at short-term (7d) survival and suggested that both eelgrass and *C. fragile* offered a similar predation refuge. Hernandez Cordero et al. (2012) compared survival over 3 weeks between two vegetated (eelgrass, *Gracilaria* sp.) and two unvegetated habitats (oyster shell, cobble) and determined that scallops within *Gracilaria* sp. exhibited intermediate survival between seagrass and unvegetated substrates. Studies which compared demographics of a native bivalve (*Anadara trapezia*) in an invasive alga (*Caulerpa taxifolia*) to bare substrate have suggested that the alga has a negative impact on the native clam (Wright et al. 2007; Wright and

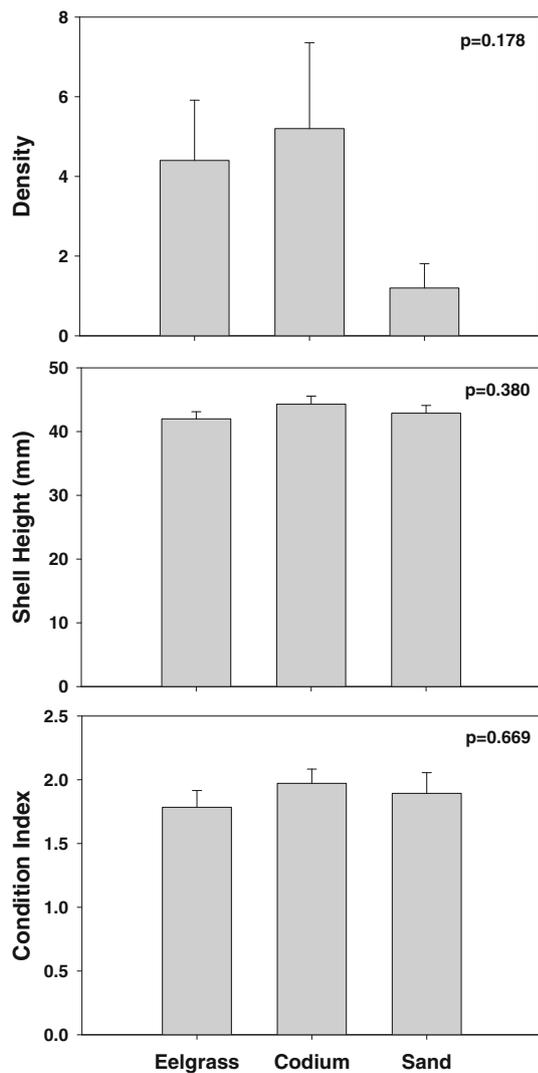


Fig. 5 Density (scallops m^{-2}), shell height (mm) and condition index using shell height for natural set scallops collected in the 3 habitats in Sag Harbor, NY, collected in November of 2010, at the same time the field experiments were ended

Gribben 2008; Gribben et al. 2009). However, unlike previous studies, we sought to compare the impacts of *Codium fragile* on bay scallop demographics with the effects of eelgrass rather than simply barren sediments since scallops frequently exhibit reduced growth and/or fitness in native, structurally complex seagrass habitats compared to barren substrates (Irlandi et al. 1995; Bologna and Heck 1999). Comparisons of these trade-offs to the ‘negative’ effects of introduced or invasive habitat formers on native species have been conspicuously absent in the literature.

In Shinnecock Bay, scallops displayed high survival, growth and condition in both vegetated habitats relative to scallops placed on bare sand, although they were not different from each other. That demographics were not different between habitats supported our hypothesis, although

we expected that scallops in the vegetation would have lower growth and condition than those on sand, as previous studies have established a food–risk trade-off for scallops between sand and seagrass (Ambrose and Irlandi 1992; Irlandi et al. 1995; Bologna and Heck 1999). The expectation that differences in scallop growth would be reflected in food quantity was not confirmed. Both whole chlorophyll *a* and $>5 \mu m$ chl *a* were highly variable across time, with samples at the sand site not having consistently different amounts of food than either eelgrass or *Codium fragile* habitats. It is probable that the enhanced growth and condition of scallops in vegetated habitats relative to barren sand was due to other factors, such as wave energy and epibiont load (Tettelbach et al. 1990, 2012).

Partial cage burial was observed at the ‘Sand’ site at Shinnecock Bay in both years; however, this phenomenon was not observed in either vegetation, suggesting that both eelgrass and *C. fragile* served to buffer wind wave activity in the relatively shallow Shinnecock Bay sites. This can have implications for scallop populations, as burial has been shown to be a significant source of overwinter mortality in scallops (Tettelbach et al. 1990). A second possible explanation for differential scallop growth and condition between scallops in the sand and the two vegetated habitats is epibiont load. Scallops in sand experienced significantly higher epibiont loads, which could restrict feeding (Tettelbach et al. 2012). However, the relationship between epibiont loading and bivalve growth is complex and varies with the species of bivalve as well as the biofouling organisms (Mallet and Carver 2009). Sea scallops, *Placopecten magellanicus*, pearl oysters, *Pinctada maxima*, and the tropical scallop, *Euvola zizac*, have been shown to experience slower growth with high epibiont loads (Clareboudt et al. 1994; Lodeiros and Himmelman 1996; Taylor et al. 1997), while growth of the oyster *Crassostrea gigas* and the bay scallop *Argopecten irradians* has been positively correlated with epibiont load (Mazouni et al. 2001; Tettelbach et al. 2012). It is possible that differences in epibiotic load between habitats caused the observed demographic patterns in scallop growth in Shinnecock Bay. Since complex habitats can reduced the transport and settlement of larvae and recruits, termed a ‘settlement shadow’ (Orth et al. 1984), differences in the amount of epibionts between the habitats may be due to the structure of the habitats.

Reproductive output, only measured in Shinnecock Bay, was different on one date between *Codium fragile* and eelgrass habitats, where scallops in *C. fragile* had higher reproductive condition, but was not different between the two habitats on all other dates, which supported our initial hypothesis. Reproduction in scallops has been shown to vary as a function many factors, such as temperature, condition, scallop size, depth, although food quantity has

received much attention (Sastry and Blake 1971; Barber and Blake 1981, 1983; Bricelj et al. 1987). Since depth, temperature, scallop size and chlorophyll were not significantly different, any one of those factors, or combinations of factors, could contribute to similarities in gonad output. Whatever the mechanism, the result that reproductive scallops did not exhibit differences in potential output among the three habitats can have important implications for scallop population persistence and growth.

Although scallops placed in the different vegetated habitats in Shinnecock Bay did not exhibit differences in measured demographics, scallops in Sag Harbor did exhibit differences as a consequence of *Codium fragile* association. Growth was lower in *C. fragile* than eelgrass in both years, and both scallop condition and survival were also lower in *C. fragile* than eelgrass in 2010. When total and $>5 \mu\text{m}$ chlorophyll *a* values were measured in 2009, there were no trends among the habitats, similar to Shinnecock Bay. Thus, the observed differences in growth and condition do not appear to be driven by food quantity. There was also no significant difference in epibiont load among the three habitats even as growth was positively related to load levels. It is possible that differences in either food quality (Milke et al. 2006) or flow (Cahalan et al. 1989) between the habitats might be responsible for the observed differences.

Food quality was not measured directly, although when chlorophyll was monitored, concentration of chlorophyll $>5 \mu\text{m}$ was used as a proxy for optimal food since scallop particle retention decreases significantly below this threshold (Riisgard 1988). Flow was also not measured, though we argue that flow may have been the explanatory factor for the observed differences in demographics. The complex *C. fragile* canopy could have reduced flow and ultimately food delivery to scallops in cages under the canopy, an issue demonstrated in other bivalve–vegetation associations (Reusch 1998; Allen and Williams 2003; Brusati and Grosholz 2007; Tsai et al. 2010). It is possible that epibiont load in Sag Harbor reflected patterns in flow within the canopies. Despite not being significantly different among the three habitats, load was highest in the sand, intermediate in grass and lowest in *C. fragile*, and there was a strong positive relationship between growth and epibiont mass. The positive relationship might reflect different fluxes between the three habitats, which would be consistent with a ‘settlement shadow’ typically observed in upright, canopy-forming vegetation. This observation suggests that new studies should examine condition across a continuum of *C. fragile* biomass and/or thalli densities to ascertain any potential threshold density that switches the impacts from beneficial to detrimental.

Density, size and condition of naturally recruiting juvenile scallops did not differ between *Codium fragile* and

eelgrass in Sag Harbor. These findings were in sharp contrast to the results of caged scallops in the second year of the study, which suggested that survival and growth of scallops should be compromised in *Codium*-invaded habitats. The reason for differences in size and condition of scallops between caged and natural scallops remains unclear, although it may reflect an experimental artifact due to caging. Since all cages were identical, the effect of caging on growth was assumed to be the same across all treatments (Connell 1974). We should have seen similar differences between natural set and caged scallops in the eelgrass and sand habitats as well if the disconnection between caged and natural set scallops was due to cages themselves.

A more likely explanation for observed differences between caged and naturally recruiting scallops may be linked to scallop behavior. Small, juvenile scallops attach to structures above the sediment surface as a predation refuge (Pohle et al. 1991), and in the benthic surveys, many natural scallops were located within and on top of the *Codium fragile* canopy, while scallops in the cages were under the canopy. It has been suggested that for the infaunal bivalve *Anadara trapezia*, behavioral modifications (‘popping-up’) in the presence of the invasive *Caulerpa taxifolia* mitigate its negative impacts (Wright et al. 2010), so the attachment behavior of scallops may afford them the ability to escape from potentially poor conditions under the *C. fragile* canopy. During this study, scallops as large as 46 mm were observed byssed to the *C. fragile* canopy—15 mm larger than the largest reported scallop byssally attached above the bottom within eelgrass (31 mm; Garcia-Esquivel and Bricelj 1993). The buoyancy of *Codium* may allow scallops to remain attached at much larger sizes than in eelgrass, keeping them in more favorable conditions. Since scallops in cages could not relocate to the *C. fragile* canopy, the differences between experimental and natural scallops were likely due to cage placement.

While there remains an incomplete understanding of the overall impacts of invasive species on native marine species (Williams and Grosholz 2008), there is a growing body of evidence suggesting that invasive submerged aquatic vegetation may be beneficial for native species (Gribben and Wright 2006; Schmidt and Scheibling 2007; Polte and Buschbaum 2008; Gestoso et al. 2010; Martin and Valentine 2011; Valinoti et al. 2011). It has even been suggested that non-native species can be tools for conservation, particularly if they provide food or shelter to rare or target native species, offer a functional substitute, or provide desirable ecosystem functions, as these species are likely to persist in the future as native species potentially become more rare (Schlaepfer et al. 2011). The studies which support positive effects of non-native species have almost

exclusively examined community metrics such as abundance and diversity and ignored demographic variables. While the studies that have investigated population demographics such as growth, condition and reproduction (Posey et al. 1993; Wright and Gribben 2008; Gribben et al. 2009; Byers et al. 2010), have shown overwhelmingly negative results, at least two recent studies suggest otherwise; urchins may receive higher-quality food in invaded habitats than native kelp habitats (Sauchyn and Scheibling 2009), and blue crabs have been demonstrated to grow as well in salt marshes invaded by *Phragmites australis* as in native habitats (Long et al. 2011). Given the ecological trade-offs exhibited by many species when associating with a complex habitat, negative impacts of invasive ecosystem engineers on fitness may be overstated.

Originally, it was proposed that in the absence of eelgrass, *Codium fragile* might be a viable replacement habitat in northwest Atlantic estuaries based on survival data (Carroll et al. 2010); the results of this study generally support such a hypothesis, albeit with some caveats. Results from this study were mixed, suggesting that the impact of *C. fragile* on bay scallop populations can probably be either ‘positive’ or ‘negative’ depending on other physical and biological factors that can vary between sites and years. Site-specific differences in the suitability of *C. fragile* as a bay scallop habitat as well as annual differences might depend on factors such as depth, current speed, weather patterns and/or percent cover of the introduced alga, among others. However, negative impacts may be over-estimated; the ‘reduced’ growth rates in *C. fragile* in this study ($\sim 0.32 \text{ mm day}^{-1}$) and resulting calculated tissue growth rates ($\sim 4.4 \text{ mg day}^{-1}$) were as high or higher than other literature values reported for scallops in Connecticut (Tettelbach 1986), Florida (Irandi et al. 1995, 1999), Massachusetts (Shriver et al. 2002), and New York (Eckman 1987; Bricelj et al. 1987; Garcia-Esquivel and Bricelj 1993; see Table 1).

In addition, scallop populations have increased dramatically in Long Island, including basins where *Codium fragile* is the dominant habitat (Tettelbach and Smith 2009; Tettelbach et al. 2013), while the decline in eelgrass has continued (Pickerell and Schott 2004). This increase is likely due to high intensity restoration efforts; however, that populations are rising in areas devoid and far removed from eelgrass meadows reinforce the hypothesis that macroalgae may serve as important and alternative habitats for bay scallops (Carroll et al. 2010; Hernandez Cordero et al. 2012). While seagrass may be a preferable habitat where available, in the absence of seagrass, *Codium fragile* may be a suitable alternative habitat for bay scallops by replacing the predation refuge function without additional biological cost. More non-native/invasive research should focus on population demographics, especially of critical

Table 1 Comparisons of scallop shell and tissue growth rates between reported literature values and results from this study, listing the demographic rate, the study location, the habitat (if available) and the authors

Shell growth rate (mm/d)	Tissue growth rate (mg/d)	Study location	Habitat	Authors
~0.2	NA	Virginia	NA	Castagna and Duggan (1971)
~0.4	NA	Florida	NA	Barber and Blake (1983)
Up to 0.33	NA	Connecticut	NA	Tettelbach (1986)
NA	4.2–6.5	New York	Seagrass/mix	Bricelj et al. (1987)
~0.28	NA	New York	Seagrass	Eckman (1987)
~0.1–0.14	NA	Florida	Seagrass	Ambrose and Irandi (1992)
0.27–0.66	~8.9 (variable)	New York	Seagrass	Garcia-Esquivel and Bricelj (1993)
0.13–0.16	NA	Florida	Seagrass	Irandi et al. (1995)
NA	Up to 0.04	Florida	Seagrass	Bologna and Heck (1999)
0.19–0.21	NA	Florida	Seagrass	Irandi et al. (1999)
0.1–0.28	NA	Massachusetts	NA	Shriver et al. (2002)
0.09–0.2	NA	Florida	NA	Geiger et al. (2006)
0.33–0.34	6.3–7.4	Shinnecock Bay, NY	Eelgrass	This study
0.33–0.34	6.4–6.8		Codium	
0.31	4.6–5.1		Sand	
0.35–0.38	6.3–7.7	Sag Harbor, NY	Eelgrass	
0.31–0.34	4.2–4.6		Codium	
0.34–0.36	5.4–8.0		Sand	

Some values are approximated from figures in the literature

fauna. Those studies should also be compared between other structured native habitats, conducted across a gradient of invader biomass, and also comparing between sites and years.

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